Eur J Appl Physiol (2011) 111:211–223
DOI 10.1007/s00421-010-1648-7

ORIGINAL ARTICLE

Comparison in eccentric exercise-induced muscle damage among four limb muscles

Trevor C. Chen · Kun-Yi Lin · Hsin-Lian Chen · Ming-Ju Lin · Kazunori Nosaka

Accepted: 3 September 2010 / Published online: 18 September 2010

Abstract This study tested the hypothesis that changes in indirect markers of muscle damage following maximal eccentric exercise would be smaller for the knee extensors (KE) and flexors (KF) compared with the elbow flexors (EF) and extensors (EE). A total of 17 sedentary men performed five sets of six maximal isokinetic (90° s^{-1}) eccentric contractions of EF (range of motion, ROM: 90°–0°, 0 = full extension), EE (55°–145°), KF (90°–0°), and KE (30°–120°) using a different limb with a 4–5-week interval in a counterbalanced order. Changes in maximal isometric and concentric isokinetic strength, optimum angle, limb circumference, ROM, plasma creatine kinase activity and myoglobin concentration, muscle soreness, and echo-intensity of B-mode ultrasound images before and for 5 days following exercise were compared amongst the four exercises using two-way repeated-measures ANOVA. All variables changed significantly following EF, EE, and KF exercises, but KE exercise did not change the optimum angle, limb circumference, and echo-intensity. Compared with KF and KE, EF and EE showed significantly greater changes in all variables, without significant differences between EF and EE. Changes in all variables were significantly greater for KF than KE. For the same subjects, the magnitude of change in the dependent variables following exercise varied among the exercises. These results suggest that the two arm muscles are equally more susceptible to muscle damage than leg muscles, but KF is more susceptible to muscle damage than KE. The difference in the susceptibility to muscle damage seems to be associated with the use of muscles in daily activities.

Keywords Lengthening exercise · Muscle strength · Optimum angle · Delayed onset muscle soreness · Flexors · Extensors

Communicated by William Kraemer.

T. C. Chen (✉) · H.-L. Chen
Department of Physical Education,
National Chiayi University, 85 Wenlong Village,
Minsyong Township, Chiayi County 62103, Taiwan
e-mail: trevorchen@mail.ncyu.edu.tw

K.-Y. Lin
Graduate Institute of Sport, and Leisure Education,
National Chung Cheng University, Chiayi County, Taiwan

M.-J. Lin
Graduate Institute of Sport Coaching Science,
Chinese Culture University, Taipei, Taiwan

K. Nosaka
School of Exercise, Biomedical and Health Sciences,
Edith Cowan University, Joondalup, WA, Australia

Introduction

Eccentric exercise induces muscle damage evidenced by the loss of strength and range of motion (ROM), delayed onset muscle soreness (DOMS), swelling and elevation of creatine kinase (CK) activity, and/or myoglobin (Mb) concentration in the blood (Clarkson and Hubal 2002; Clarkson et al. 1992; Hirose et al. 2004). As a model to investigate eccentric exercise-induced muscle damage, exercises consisting of maximal or submaximal isokinetic eccentric contractions of the elbow flexors or knee extensors have been often used in previous studies. However, it has been reported that damage profile is different between muscles, and the knee extensors are less susceptible to eccentric exercise-induced muscle damage than the elbow flexors (Jamurtas et al. 2005; Saka et al. 2009).

Jamurtas et al. (2005), compared an elbow flexor (EF) exercise and a knee extensor (KE) exercise consisting of submaximal (75% of predetermined maximal eccentric peak torque) isokinetic (60° s^{-1}) eccentric contractions (6 sets of 12 repetitions) from 135° to 0° (full extension = 0°) for the EF and from 0° to 120° for the KE. They showed significantly smaller increases in serum CK activity and Mb concentration, and smaller decrease in muscle strength for the KE compared with the EF, but no significant differences between the muscles were observed for the change in ROM and DOMS following exercise. Saka et al. (2009) reported that decreases in isometric strength and ROM, increases in serum CK activity and Mb concentration, and DOMS were significantly smaller for the KE compared with the EF, when 3 sets of 15 maximal isokinetic (30° s^{-1}) eccentric contractions were performed by the muscles for the same ROM (90°–0° for the EF, 0°–90° for the KE). These authors speculated that differences in the use of the muscles in daily activities, force–length relationship, muscle architecture, and muscle fibre composition were associated with the difference in the susceptibility to eccentric exercise-induced muscle damage between the muscles (Jamurtas et al. 2005; Saka et al. 2009).

Less number of studies has investigated other muscle groups for their susceptibility to eccentric exercise. To the best of our knowledge, only one study compared two leg muscle groups. Franklin et al. (1993) examined the KE and knee flexors (KF) for changes in plasma CK activity and muscle soreness following 3 sets of 35 maximal isokinetic (120° s^{-1}) eccentric contractions. They reported that increases in plasma CK activity and muscle soreness were significantly greater for the KF compared with the KE. However, other markers of muscle damage were not measured in the study. No previous studies have systemically compared between the elbow extensors (EE) and the KF, or EF and KE for their responses to maximal eccentric contractions.

If leg muscles were less susceptible to eccentric exercise-induced muscle damage than arm muscles as discussed in the previous studies (Jamurtas et al. 2005; Saka et al. 2009), a difference in the magnitude of muscle damage would also be observed between the EE and KF. We hypothesised that changes in indirect markers of muscle damage following maximal eccentric exercise would be smaller for KF and KE compared with the EF and EE, without significant difference between the arm muscles, and the leg muscles. To test the hypothesis, the present study compared the EF and EE, and KF and KE using four different limbs of the same subjects.

Methods

Subjects

All subjects were screened for their medical history and physical activities in the past year. A total of 17 young sedentary male students, who had not performed regular resistance, aerobic or flexibility training in the past one year, and who had not carried heavy objects or climbed up and down stairs regularly in their daily activities, were recruited for the present study. They had no previous muscle, joint or bone injuries of the upper or lower extremities and were considered to be "healthy" individuals. We judged their suitability to participate in the study based on the information that they provided, and the present study did not monitor actual physical activities prior to and during the experimental period. They provided informed consent to participate in this study that had been approved by the Institutional Ethics Committee. The study was conducted in conformity with the policy statement regarding the use of human subjects by the Declaration of Helsinki.

Their mean (±SD) age, height, and body mass were 21.1 ± 2.1 years, 175.1 ± 4.6 cm, and 71.4 ± 9.9 kg, respectively. The subjects were asked and reminded to refrain from unaccustomed exercise or vigorous physical activity and maintain their normal dietary habits, and not to take any anti-inflammatory drugs (e.g. non-steroid anti-inflammatory drugs) or nutritional supplements (e.g. vitamins, protein/amino acids) during the experimental period. The subjects were instructed to drink enough water after exercise to avoid a possible risk of acute renal failure due to rhabdomyolysis, refrain from alcohol, and not to have any treatments of the exercised muscles (e.g. massage, stretching) during the study. The number of subjects was determined by a sample size estimation using the data from previous studies (Jamurtas et al. 2005; Saka et al. 2009) in which maximal eccentric exercises of the EF and KE were compared. The estimation was based on the effect size of 1, alpha level of 0.05, a power ($1 - \beta$) of 0.80, and an expected difference of 10% for the difference in muscle strength recovery at 3 days post-exercise, and it was shown that at least 12 subjects were necessary.

Experimental design and eccentric exercise

All subjects performed a bout of eccentric exercise of the EF, EE, KF, and KE separated by 4–5 weeks using a different limb in a counterbalanced order (Fig. 1), and the use of dominant and non-dominant limbs was also counterbalanced among subjects to minimise the possible order

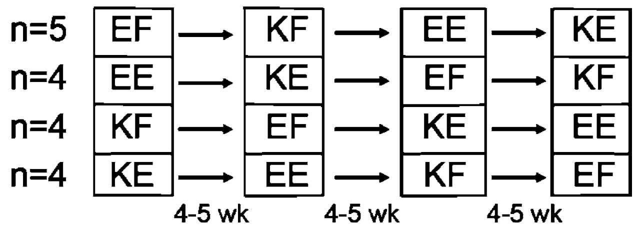

Fig. 1 Study design and the randomisation of the order of eccentric exercises of the elbow extensors (EE) and flexors (EF), and knee extensors (KE) and flexors (KF). For example, 5 subjects started from the elbow flexor exercise (e.g. right arm), followed by knee flexors (e.g. right leg), elbow extensors (e.g. left arm), and knee extensors (e.g. left leg)

effect. The exercise was performed between 09:00 and 16:00, and each subject performed the four exercises at the same time of the day (within 4-h difference). Since it has been shown that only a few maximal eccentric contractions produce some protective effect against eccentric exercise-induced muscle damage (Nosaka et al. 2001), the subjects did not perform any eccentric contractions in a familiarisation that was set 3 days prior to each exercise bout. However, each exercise was demonstrated to the subjects in the familiarisation session, and they performed several concentric contractions and received other measures (ROM, muscle soreness) in the session.

Each exercise consisted of five sets of six maximal isokinetic eccentric contractions at the angular velocity of 90° s^{-1} (1.57 rad s^{-1}) on an isokinetic dynamometer (Biodex Pro 3 System, Shirley, NY, USA) based on the exercise protocol of the EF used in previous studies (Newton et al. 2008; Chen et al. 2009). In the present study, the same number of maximal eccentric contractions (i.e., 30 contractions) was set for the four exercises, although previous studies (Crameri et al. 2007; Dudley et al. 1997; Golden and Dudley 1992; Franklin et al. 1993) used a larger number of eccentric contractions especially for the KE (e.g. 70–210 contractions) or KF (e.g. 105 contractions). To standardise the velocity of eccentric contractions and ROM, and to quantify the torque and work during eccentric exercise, an isokinetic dynamometer was used in this study. The body positioning was based on the instructions of the dynamometer for each exercise, and the trunk and the limb of the subject were stabilised by straps accordingly.

Figure 2 shows the four eccentric exercises performed in the present study. For the EF and EE exercises, the shoulder joint angle was set at 90° flexion with 0° abduction, and the forearm was supinated with the arm holding the lever attachment of the dynamometer. For the KF and KE exercises, the subject was seated with his hip joint at 85° of flexion, and the arms were folded in front of the chest. Using the dynamometer's software, the gravitational correction was made for EF, EE, KF, and KE at 20°, where the anatomical zero was set at the angle of fully extending the limb. The ROM was 90° for all exercises, but the starting and finishing angle were different amongst the exercises, such as 90° and 0° for the EF, 55° and 145° for the EE, 30° and 120° for the KE, and 90° and 0° for the KF, where the anatomical zero was considered as 0° (Fig. 2). Each eccentric contraction was performed after a 1-s maximal isometric contraction at the starting angle. A 10-s rest was given between contractions during which the limb was returned to the stating angle passively by the isokinetic dynamometer (9° s^{-1}), and 2-min rest was given between sets. Subjects were verbally encouraged to generate maximum force in each contraction for whole ROM.

Criterion measures

Dependent variables consisted of maximal voluntary isometric contraction (MVC-ISO) and isokinetic concentric strength at 60° s^{-1} (MVC-CON), optimum angle, ROM, limb circumference, plasma CK activity and Mb concentration, muscle soreness, and echo intensity of B-mode ultrasound images. These variables were chosen because they have been often used as indirect markers of muscle damage in previous studies (e.g. Chen et al. 2009). The measurements were taken 2 days and immediately before exercise, immediately after, and 1, 2, 3, 4, and 5 days post-exercise for all variables except for muscle soreness, plasma CK activity and Mb concentration, and the ultrasound images. The muscle soreness, CK, and Mb measures were not included at the immediately post-exercise time point, and the ultrasound images were recorded before exercise, 2 and 5 days after exercise only. Based on the two baseline measures (2 days and immediately before exercise), the test–retest reliability of the measures was examined.

MVC-ISO, MVC-CON, and optimum angle

MVC-ISO was measured at three different angles, such as 50°, 70°, and 90° for EF; 90°, 110°, and 130° for EE; 10°, 30°, and 50° for KF; and 70°, 90°, and 110° for KE, with the same set up as the exercise using the dynamometer after gravity correction. The order of the testing angles was standardised from a short muscle length to a long muscle length. The subjects were instructed to generate maximal force for 3 s at each angle for 3 times with a 45-s rest between trials, and a 2-min rest between angles. Verbal encouragement was provided in a consistent manner during all tests. The highest value of the three trials was used for further analysis.

MVC-CON and optimum angle were measured at the angular velocity of 60° s^{-1} (Brockett et al. 2001; Bowers

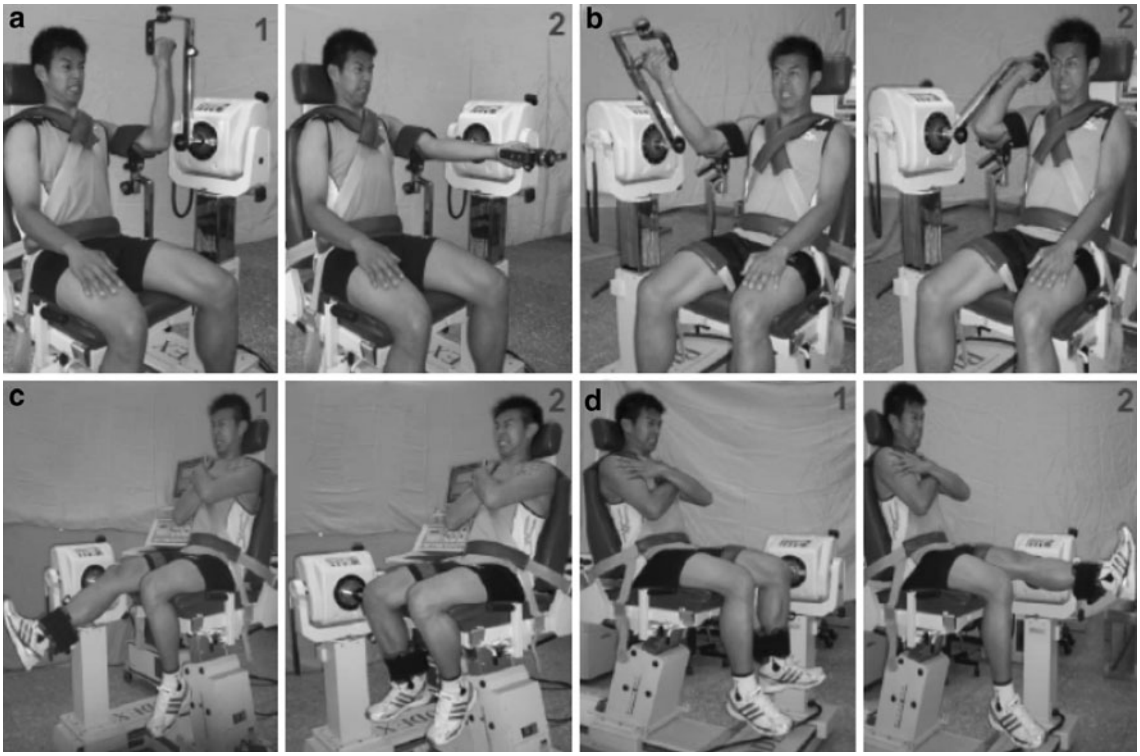

Fig. 2 Eccentric exercise of the elbow flexors (**a**) and extensors (**b**), and the knee extensors (**c**) and flexors (**d**). For each exercise, the starting (*1*) and finishing (*2*) joint angles of eccentric contraction are shown

et al. 2004; Cramer et al. 2007) for the ROM of 140° for the EF (0°–140°) and EE (140°–0°), or 120° for the KF (0°–120°) and KE (120°–0°) for three continuous maximal voluntary concentric contractions for both directions. The angular velocity was based on the previous studies in which the optimum angle of the knee flexors (Brockett et al. 2001) or knee extensors (Bowers et al. 2004) was examined. The torque, position (joint angle), and displacement signals of each contraction were saved in a computer connected to the isokinetic dynamometer, the raw data were filtered and smoothed, and peak torque and the joint angle of the peak torque (optimum angle) were analysed by the software of the Biodex Medical Systems. The average of the three trials was used for subsequent analysis.

ROM

ROM was determined as the difference in the joint angles between voluntary maximal flexion (FANG) and extension (EANG) of elbow or knee joint. For the EF and EE, the FANG was measured when the subject maximally tried to touch his shoulder of the same side by flexing the elbow joint while keeping the elbow joint at the side of the body in a standing position. The EANG was measured when the subject attempted to extend his elbow joint as much as possible with the elbow held by his side and the hand in mid-pronation. For the KE and KF, FANG was measured when the subject tried to maximally flex the knee joint to touch his hip by the heel while keeping the knee joint at the side of the body in a stand position and other leg being used to stabilize the position. EANG was determined when the subject attempted to extend his knee joint as much as possible with the knee held by his side. A plastic goniometer was used for the measures, and three measurements were taken for each angle, and the average of the three measurements was used to calculate ROM by subtracting FANG from EANG.

Limb circumference

The circumference of the exercise limb was measured at the mid-portion of each limb (Perotto1994) using a Gulick tape measure, while the subject relax and let the arm hang down by the side or stood with the non-exercise leg and held the exercise leg relaxed. For the mid-upper arm circumference measures, the perimeter distance of the upper arm perpendicular to the long axis of the humerus was measured from the marked site made by a semipermanent ink pen (Chen et al. 2007; Hawes and Martin 2001). For the mid-thigh circumference, the perimeter distance of the thigh perpendicular to the long axis of the femur at the marked mid-trochanterion-tibiale level was measured (Hawes and Martin 2001). The measurements were made three times for each time point, and the average of the three measures was used for statistical analysis. The same investigator took all measurements.

Muscle soreness

Muscle soreness was quantified using a visual analogue scale (VAS) that had a 100-mm continuous line with "not sore at all" on one side (0 mm) and "very, very sore" on the other side (100 mm) (Chen and Nosaka 2006; Chen et al. 2007). The investigator asked the subject to rate his perceived soreness on the VAS when the muscles were passively extended and flexed for the ROM that was used for the MVC-CON measures.

Plasma CK activity and Mb concentration

Approximately 7-ml of venous blood was withdrawn by a standard venipuncture technique from the cubital fossa region of the arm and centrifuged for 10 min to extract plasma, which was stored at −80°C until analyses. Plasma CK activity was assayed spectrophotometrically by an automated clinical chemistry analyser (Model 7080, Hitachi, Co. Ltd., Tokyo, Japan) using a commercial test kit (Roche Diagnostics, Indianapolis, IN, USA). Plasma Mb concentration was measured by an automated clinical chemistry analyser (Model Elecsys 2010, F. Hoffmann-La Roche Ltd., Tokyo, Japan) using a commercial test kit (Roche Diagnostics, Indianapolis, IN, USA). Each sample was analysed in duplicate, and the average value of two measures was used for subsequent statistical analysis. The normal reference ranges for plasma CK activity and Mb concentration in men using the method are 38–174 IU l^{-1} and <110 μg l^{-1}, respectively, based on the manufacturer's information.

Ultrasonography

The procedures of the echo intensity assessment were adopted from the previous studies (Chen et al. 2009; Nosaka and Clarkson 1996; Nosaka and Newton 2002). Briefly, an ultrasound probe was placed on a marked site on a muscle belly with the same angle and pressure over days to get a B-mode ultrasound image, and echo-intensity of a region of interest was assessed using an image analysis software. In the present study, the ultrasound images of the exercised muscles were taken using a Terason t3000 Ultrasound System with a 7.5-MHz linear probe (Terason Co., Burlington, MA, USA). The probe was placed at the mid-portion of the biceps brachii, long head of the triceps brachii, rectus femoris, and biceps femoris, respectively, as the same sites of the limb circumference measurements. The subject was sitting on a chair with the forearm on a padded table at the shoulder angle of 80° and the elbow joint angle of 170° for the elbow flexor measures. For the elbow extensor measures, the subject was lying prone on a padded table with the shoulder abducted to about 50° and the elbow joint was about 150°. For the knee extensor measures, the subject was lying supine on a padded table with the hip, knee, and ankle joints angle of 0° (i.e., neutral position), and the subject was lying prone with the hip, knee, and ankle joints angle of 0° (i.e., neutral position) for the knee flexor measures. Placement of the ultrasound probe and the volume of the ultrasound gel were standardised, and the same investigator took all images. The transverse images were obtained from the same sites over time, while keeping the focus, gain, and contrast and other setting of the ultrasound machine unchanged over days, and all images were saved in a computer (HP Workstation xw4400, Singapore). Based on the previous study (Chen et al. 2009), the saved images were analysed by a computer image analysis software (ULT File Reader for Windows, Broadsound Co., Taiwan), and the mean echo intensity of a histogram of gray scale (0: black, 256: white) was calculated for the region of interest (ROI: $2 \times 2 = 4$ cm^2). The ROI was set approximately 5 mm adjacent to the humerus for the biceps brachii and triceps brachii, and the femur for the rectus femoris and biceps femoris. The relative change in the echo intensity from the pre-exercise value was calculated.

Reliability

The test–retest reliability of the dependent variables was determined by an intraclass correlation coefficient (R) using the two baseline measures taken at 2 days and immediately before the exercise. The R values for MVC-ISO, MVC-CON, optimum angle, ROM, limb circumference, muscle soreness, and plasma CK activity and Mb concentration among the muscles was 0.92–0.98, 0.91–0.97, 0.91–0.96, 0.90–0.97, 0.98–0.99, 1.00, 0.84–0.91, and 0.88–0.92, respectively. The coefficient of variation for MVC-ISO, MVC-CON, optimum angle, ROM, limb circumference, muscle soreness, and plasma CK activity and Mb concentration among the muscles was 7.7–9.3, 6.4–9.0, 5.3–10.1, 3.6–7.2, 5.7–5.9, 0, 8.6–10.2, and 6.9–8.8%, respectively.

Statistical analyses

Changes in each criterion measure over time (before, immediately after, and 1–5 days after eccentric exercise) were analysed by one-way repeated-measures analysis of variance (ANOVA). When a significant time effect was found, a Tukey's post hoc test was followed to locate a significant difference from the baseline value. Changes in the criterion measures over time were compared amongst the four exercises (i.e., EF, EE, KF, and KE) by a two-way ANOVA. If a significant interaction (exercise × time) effect was detected, a series of two-way ANOVA was performed separately to compare two exercises (EF vs. EE, EF vs. KF, EF vs. KE, EE vs. KF, EE vs. KE, and KE vs. KF) followed by a Tukey's post hoc test when a significant interaction effect was found. To check a possible order effect, a two-way ANOVA was performed to compare four sub-groups of subjects who performed the same exercise (e.g. EF) as the first, second, third, or fourth bout (Fig. 1). The 95% confidence intervals of the criterion measures before each exercise and torque and work during each eccentric exercise were obtained. Statistical significance was set at $P \leq 0.05$. Data are presented as mean ± SEM, unless otherwise stated.

Results

Baseline values

The baseline values of the dependent variables are shown in Table 1. Significant differences between the EE, EF and KE, KF were observed for the pre-exercise values of MVC-ISO, MVC-CON, ROM and circumference, and significant differences were also evident between the EE and EF for optimum angle and echo-intensity, and between KE and KF for optimum angle, MVC-ISO, and MVC-CON. No significant differences amongst the four different muscles were seen for muscle soreness, CK, and Mb.

Peak torque and work during eccentric exercise

The average peak torque produced during 30 eccentric contractions was significantly greater for KF and KE compared with EF and EE, and no significant difference was evident between EF and EE, but the torque was significantly greater for KE than KF (Table 1). The average torque divided by the pre-exercise MVC-ISO was 98 ± 3% for EF, 94 ± 4% for EE, 102 ± 5% for KF, and 107 ± 7% for KE, and a significant difference was evident between EE and KF, EE and KE, and EF and KF. The total work during eccentric exercise was significantly greater for KE and KF compared with EF and EE, with a significantly greater work for KE than KF (Table 1).

Optimum angle and muscle strength

As shown in Fig. 3a, optimum angle changed significantly for EF, EF and KF with the greatest shift to a longer muscle

Table 1 Baseline values (means ± SEM, 95% confidence interval) of optimum angle, maximal voluntary concentric strength (MVC-CON), maximal voluntary isometric strength (MVC-ISO) at the angle that showed the highest value, range of motion (ROM), limb circumference, muscle soreness, plasma creatine kinase activity (CK), myoglobin concentration (Mb), and echo intensity for the elbow flexors (EF) and extensors (EE), and knee flexors (KF) and extensors (KE)

	EF	EE	KF	KE
Optimum angle (°)	76.8 ± 2.0 (72.4–81.1)	108.5 ± 2.1 (103.2–113.9)	45.5 ± 3.2 (37.2–53.7)	73.5 ± 2.2 (67.8–79.2)
MVC-CON (Nm)	32.5 ± 2.0 (30.6–34.3)	33.4 ± 2.3 (30.4–36.4)	68.5 ± 7.2 (59.2–77.8)	140.3 ± 15.2 (120.7–159.8)
MVC-ISO (Nm)	46.8 ± 3.4 (43.5–52.1)	47.9 ± 4.2 (42.5–53.3)	108.3 ± 7.1 (96.2–120.4)	204.4 ± 18.5 (175.9–233.0)
ROM (°)	140.5 ± 1.7 (138.2–143.4)	138.8 ± 2.8 (134.6–141.4)	105.8 ± 2.0 (103.9–109.3)	107.2 ± 2.9 (101.1–113.6)
Circumference (mm)	273.1 ± 6.4 (256.6–289.6)	272.3 ± 6.3 (255.9–288.6)	535.4 ± 12.3 (503.8–567.1)	547.1 ± 12.4 (515.1–579.0)
Muscle soreness (mm)	0 ± 0	0 ± 0	0 ± 0	0 ± 0
CK (IU/l)	138.2 ± 9.8 (117.5–158.8)	124.6 ± 10.4 (102.6–146.7)	120.1 ± 10.3 (98.2–142.0)	124.4 ± 9.6 (104.0–144.8)
Mb (μg/l)	25.9 ± 1.2 (22.0–30.2)	27.2 ± 1.6 (23.1–31.3)	27.9 ± 1.7 (23.5–32.4)	25.5 ± 1.5 (21.6–29.4)
Echo intensity	53.4 ± 2.0 (47.9–56.6)	77.9 ± 1.4 (67.7–82.8)	89.0 ± 1.2 (78.1–93.4)	78.7 ± 1.7 (68.8–83.2)
Torque (Nm)	45.8 ± 2.1 (44.4–47.3)	44.8 ± 2.2 (41.5–48.1)	116.0 ± 11.4 (102.3–129.7)	208.2 ± 21.9 (183.0–233.5)
Work (J)	1546.4 ± 20.7 (1493.1–1599.7)	1593.6 ± 45.9 (1475.7–1711.6)	4395.6 ± 214.3 (3544.5–4646.6)	7019.1 ± 414.3 (5954.0–8084.2)

Peak torque (Torque) and total work (Work) during the eccentric exercise are also shown

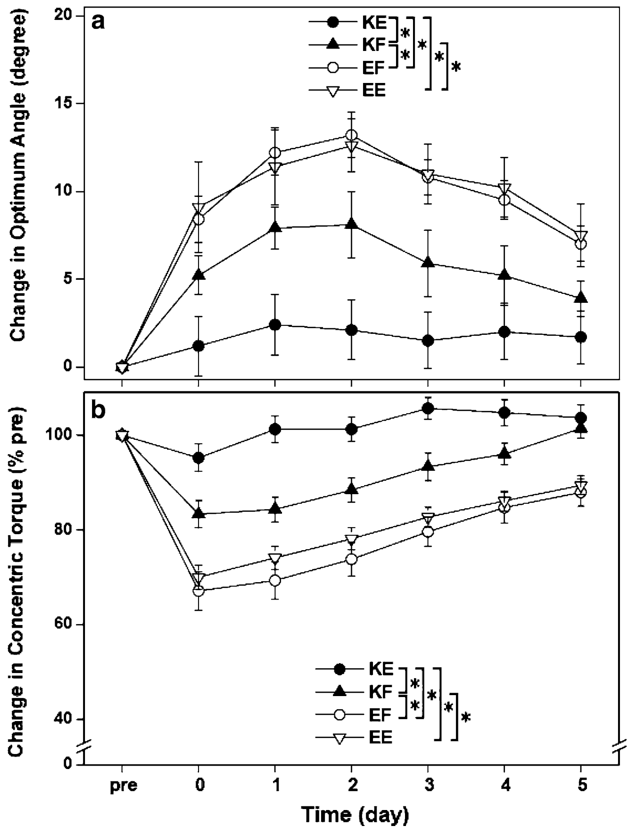

Fig. 3 Changes in optimum angle (**a**) and maximal voluntary isokinetic concentric contraction strength at the optimum angle (**b**) before (pre), immediately after (post) and 1–5 days after maximal eccentric exercise of the elbow flexors (EF) and extensors (EE), and knee flexors (KF) and extensors (KE; means ± SEM). An *asterisk* (*) indicates a significant difference ($P < 0.05$) between exercises based on the interaction effect shown by the ANOVA

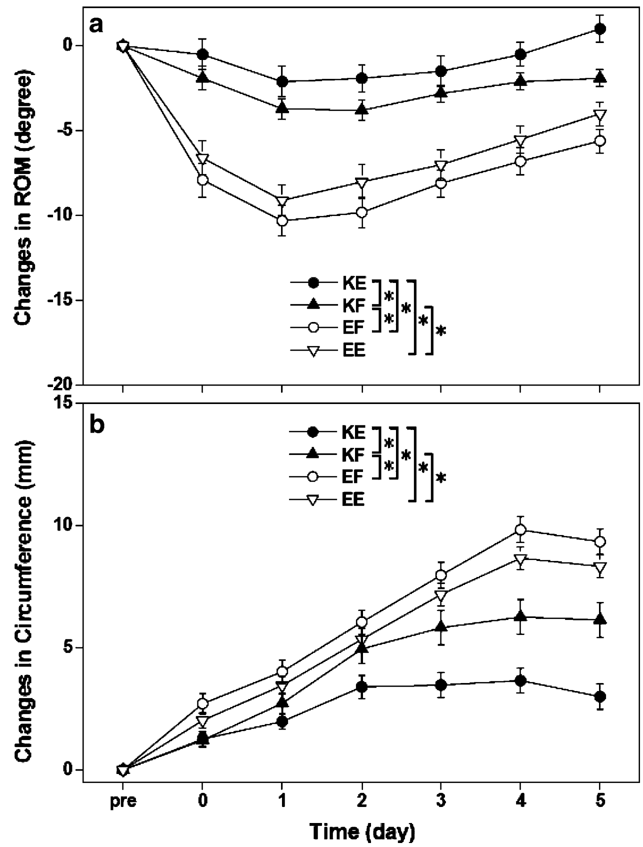

Fig. 4 Changes in range of motion (**a**) and limbs circumference (**b**) before (pre), immediately after (post) and 1–5 days after maximal eccentric exercise of the elbow flexors (EF) and extensors (EE), and knee flexors (KF) and extensors (KE; means ± SEM). An *asterisk* (*) indicates a significant difference ($P < 0.05$) between exercises based on the interaction effect shown by the ANOVA

length at 1–2 days post-exercise, but no significant change was seen for KE. The changes in the optimum angle were significantly greater for EF and EE compared with KE and KF, without a significant difference between EF and EE, but with a significant difference between KF and KE. Figure 3b shows changes in MVC-CON at the optimum angle. MVC-CON decreased significantly immediately after exercise for EF (33 ± 4%), EE (30 ± 3%), KF (17 ± 2%), and KE (5 ± 2%), and the magnitude of the decrease was significantly greater for EE and EF compared with KE and KF, without a significant difference between EF and EE, but with a significant difference between KF and KE. MVC-CON returned to the baseline significantly faster for KF and KE compared with EF and EE, with a significantly faster recovery for KE than KF, and without a significant difference between EF and EE. The changes in MVC-ISO at the three angles were similar to those of MVC-CON, although the absolute values of MVC-ISO at the three angles were larger than those of MVC-CON values, and the differences in MVC-ISO among the angles were small.

The individual responses of MVC-CON to each eccentric exercise are shown in Fig. 7a. A large variability among the subjects was seen for all exercises; however, it is interesting to note that the subjects who showed large decreases in MVC-CON following one exercise (e.g. EF) did not necessarily show large decreases in MVC-CON for other exercises (e.g. EE, KF, and KF).

ROM and limb circumference

ROM decreased significantly after eccentric exercise for EF (10° ± 2°), EE (10° ± 2°), and KF (4° ± 1°), KE (2° ± 1°). The changes were significantly greater for EF and EE compared with KF and KE, without a significant difference between EF and EE, and with a significant difference between KE and KF (Fig. 4a). Significant increases in the limb circumference were evident for EF, EE, and KF, and the increase was significantly greater for EF and EE compared with KF, without a significant difference between EF and EE (Fig. 4b).

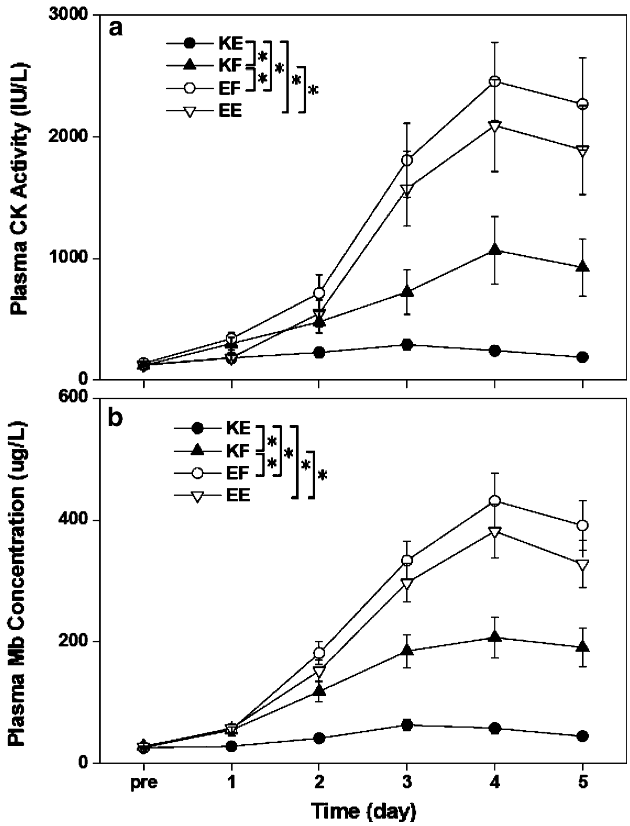

Fig. 5 Changes in plasma creatine kinase (CK) activity (**a**) and myoglobin (Mb) concentration (**b**) before (pre) and 1–5 days after maximal eccentric exercise for the elbow flexors (EF) and extensors (EE), and knee flexors (KF) and extensors (KE; means ± SEM). An *asterisk* (*) indicates a significant difference ($P < 0.05$) between exercises based on the interaction effect shown by the ANOVA

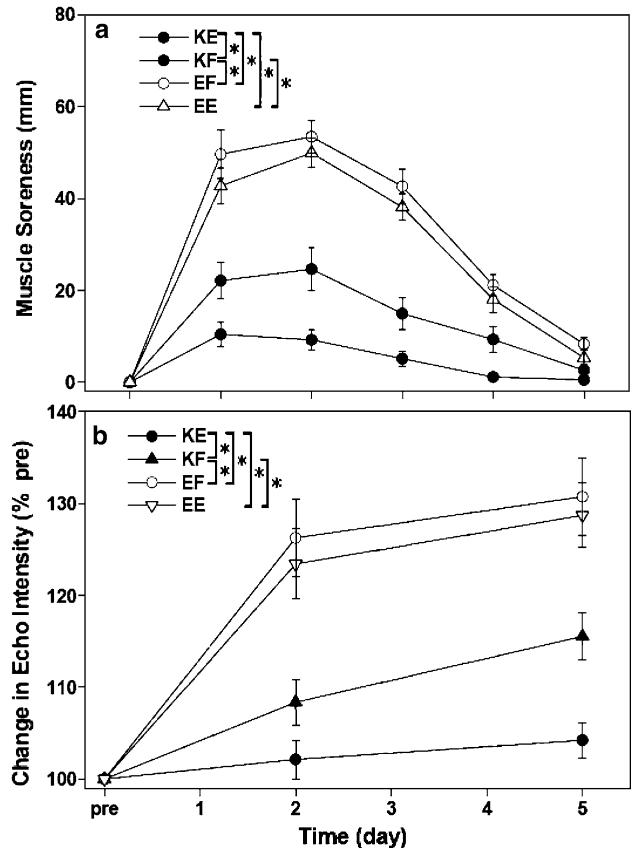

Fig. 6 Changes in muscle soreness (**a**) and echo intensity of B-mode ultrasound (**b**) before (pre), immediately after (post), and 1–5 days (2 and 5 days for ultrasound) after maximal eccentric exercise of the elbow flexors (EF) and extensors (EE), and knee flexors (KF) and extensors (KE; means ± SEM). An *asterisk* (*) indicates a significant difference ($P < 0.05$) between exercises based on the interaction effect shown by the ANOVA

Plasma CK activity and Mb concentration

Significant increases in plasma CK activity and Mb concentration were evident after eccentric exercise for all exercises; however, the increases were significantly greater for EF and EE than for KF and KE, without a significant difference between EF and EE, but the increases were significantly greater for KF than KE (Fig. 5). The individual responses of plasma CK activity to each eccentric exercise are demonstrated in Fig. 7b. As the case for MVC-CON explained above, the subjects who showed large increases in plasma CK activity following one exercise (e.g. EF) did not necessarily show large increases in plasma CK activity for other exercises (e.g. EE, KF, and KF).

Muscle soreness

As shown in Fig. 6a, the magnitude of muscle soreness developed after exercise was significantly greater for EF and EE compared with KF and KE, without a significant difference between EF and EE, and the muscle soreness of KF was significantly greater than that of KE. The individual responses of muscle soreness to each eccentric exercise are shown in Fig. 7c. The subjects who had severe muscle soreness following one exercise (e.g. EF) did not necessarily experience severe muscle soreness after other exercises (e.g. EE, KF, and KF).

Echo intensity

Echo intensity increased significantly following EF, EE, and KF, but not for KE (Fig. 6b). The increases in echo intensity were significantly greater for EF and EE compared with KF and KE, without a significant difference between EF and EE, and with a significantly greater increase for KF than for KE.

Effect of the exercise order

Using sub-groups of subjects ($n = 4$–5) who performed the same exercise in a different order (Fig. 1), changes in all dependent variables following exercise (e.g. EF) were compared among the groups for each variable separately. No

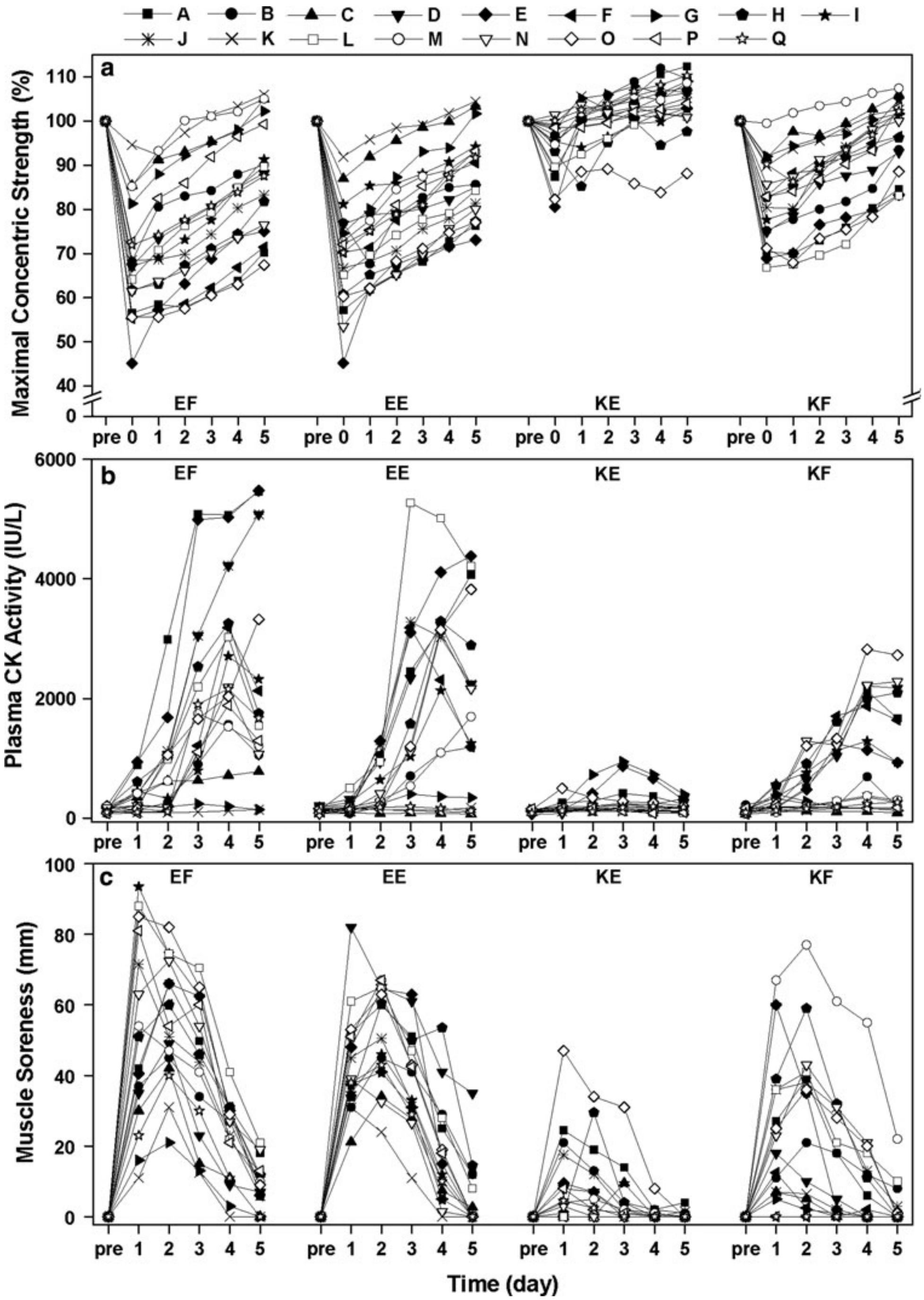

Fig. 7 Individual subject responses ($n = 17$) to maximal eccentric exercise of elbow flexors (EF) and extensors (EE), and knee extensors (KE) and flexors (KF) for some selected dependent variables. Normalised changes in maximal concentric strength from baseline (*a*), changes in plasma creatine kinase (CK) activity (**b**), and muscle soreness (**c**) before (pre), immediately after (0), and 1–5 days after each eccentric exercise are shown

significant differences in the changes in the dependent variables were observed among the bouts for any of the exercises (EF, EE, KE, and KF). This was also the case for the average torque and work produced during eccentric contractions.

Discussion

The results showed that the magnitude of changes in all dependent variables was significantly greater for EF and EE compared with KF, without significant differences between EF and EE, and KE showed significantly smaller changes in all variables than others. These results confirmed the findings of the previous studies reporting that muscle damage was less for KE compared with EF (Jamurtas et al. 2005; Saka et al. 2009), and muscle damage was greater for KF than KE (Franklin et al. 1993). New findings were that muscle damage was similar between EF and EE, the arms muscles (EF and EE) were more susceptible to muscle damage than KF, and the magnitude of muscle damage was different among the muscles even within the same individuals.

The changes in the dependent variables following the eccentric exercise of KE in the present study were not as large as those reported in some of the previous studies. It should be noted that the previous studies (Black and McCully 2008; Crameri et al. 2007; Dudley et al. 1997; Paschalis et al. 2005) reporting larger decreases in muscle strength following eccentric exercise of KE used a larger number of eccentric contractions (e.g. 70–210) compared with that of the present study (30 contractions). The eccentric contraction velocities varied (30°–180° s^{-1}) among the previous studies (Crameri et al. 2007; Jamurtas et al. 2005; Paschalis et al. 2005). Chapman et al. (2008) reported that fast velocity eccentric contractions (210° s^{-1}) resulted in greater muscle damage than slow velocity eccentric contractions (30° s^{-1}) of the EF when the number of eccentric contractions was large (i.e. 210 contractions). Thus, the smaller number of eccentric contraction was the main reason for the smaller magnitude of muscle damage following the KE exercise in the present study. The present study compared the four limb exercises by matching the number of contractions and ROM (i.e. 90°), which was a limitation of the present study.

Jamurtas et al. (2005) did not find a significant difference between KE and EF for changes in ROM and muscle soreness. However, the present and previous studies (Saka et al. 2009) found a significant difference in ROM and muscle soreness between KE and EF eccentric exercises (Figs. 4, 6). A difference in the assessment protocol for ROM and muscle soreness might explain the different findings. In the study by Jamurtas et al. (2005), ROM was measured passively using an isokinetic dynamometer, and muscle soreness was assessed by self-palpation. For the comparison between EF and KE, the results of the present study confirmed the findings of the study by Saka et al. (2009), although there were some differences in the exercise protocols between studies.

Only one previous study (Franklin et al. 1993) compared KE and KF for their responses to eccentric exercise, but the muscle damage markers were limited to plasma CK activity and muscle soreness. They reported that the increases in plasma CK activity and muscle soreness following 3 sets of 35 isokinetic (120° s^{-1}) eccentric contractions were significantly greater for the KF compared with the KE. The present study found similar results (Figs. 5, 6), and showed that changes in optimum angle, muscle strength, ROM, circumference, Mb, and echo intensity were also significantly greater following exercise of KF than KE (Figs. 3, 4, 5, 6). The changes in these variables following KF eccentric exercise in the present study were similar to those reported in a previous study (Brockett et al. 2001). When comparing the changes in the dependent variables following eccentric exercise of the KF with those reported after eccentric exercise of the KE in previous studies (Crameri et al. 2007; Dudley et al. 1997) that showed greater changes in muscle damage markers than those of the present study, it appears that the changes are still greater for the KF compared with KE. Thus, it seems that KF is more susceptible to eccentric exercise-induced muscle damage than KE, generally.

To the best of our knowledge, no previous study reported changes in muscle damage markers following eccentric exercise of EE, although many studies used EF (e.g. Byrne et al. 2004; Clarkson and Hubal 2002; Clarkson et al. 1992; Hirose et al. 2004). The magnitude of muscle damage of EF vary among the studies; however, the changes in the criterion measures shown in the present study following EF exercise (Figs. 3, 4, 5, 6) are similar to those reported in some of the previous studies (Byrne et al. 2004; Clarkson and Hubal 2002; Clarkson et al. 1992; Hirose et al. 2004). No significant differences in the changes in any of the criterion measures between EF and EE (Figs. 3, 4, 5, 6) suggest that the two arm muscles are equally susceptible to eccentric exercise-induced muscle damage.

These results raise a question why the susceptibility to eccentric exercise-induced muscle damage is different between EF/EE and KF/KE and between KF and KE, but similar between EF and EE. The difference in the magnitude of muscle damage between leg muscle (KF, KE) and the arm muscles (EF, EE) may be explained by a difference in exposure to eccentric contractions in daily activities. Jamurtas et al. (2005) and Prior et al. (2001) speculated that submaximal eccentric loading during daily activities, such as downhill walking, going downstairs, and sitting down make the leg muscles more resilient to eccentric exercise-induced muscle damage. It has been well documented that the magnitude of eccentric exercise-induced damage is attenuated once muscles are exposed to eccentric contractions, which is known as the repeated bout effect (Clarkson et al. 1992; McHugh 2003; McHugh et al. 1999). Newton et al. (2008) reported that resistance-trained individuals had little muscle damage following maximal eccentric exercise of the EF that they had not experienced in their training. It seems likely that KE are accustomed eccentric contractions from daily activities as seen in the resistance-trained individuals. It is speculated that leg muscles are generally more exposed to eccentric contractions in daily activities than arm muscles. However, in the present and previous studies (Jamurtas et al. 2005; Prior et al. 2001; Saka et al. 2009), no quantitative analyses of muscle activities of the limb muscles in daily activities were performed. Thus, it should be investigated further, how much difference in muscle activities especially eccentric contractions in daily activities exist among muscles.

It should be noted that the extent of muscle damage was significantly different between KF and KE. It is possible that a difference in the frequency of eccentric contractions in daily activities, a difference in muscle length changes during the eccentric contractions in the exercise protocol of the present study, and a difference in muscle architecture explain the difference in the muscle damage. It is possible that KE is exposed to even more eccentric contractions than KF in daily activities as proposed by Franklin et al. (1993). Regarding the muscle length, the muscles were not fully extended in the KE exercise (30°–120°), but extended to the end of ROM in the KF exercise (90°–0°) in the present study (Fig. 2). It is possible that muscle strain was greater for KF than KE due to the greater usage of the muscles in the descending limb for the former than the latter. Figure 8 shows the possible muscle length changes in the ROM used in the exercise in the present study. It should be noted that the difference in the eccentric contractions performed in the descending limb range is not largely different among the exercises. However, it should be noted that the effects of other joints are not accounted for in the figure. For example, it has been reported that changing the hip joint angle affect the movement arm of lower limb muscles (e.g. biceps femoris) more than the knee joint angle (Chelboun et al. 2001; Visser et al. 1990). Thus, the actual muscle length–angle relationship and actual changes in muscle lengths during eccentric contractions are not known. Further investigation to delineate the muscle length–angle relationship together with force–length relationship in each exercise is necessary.

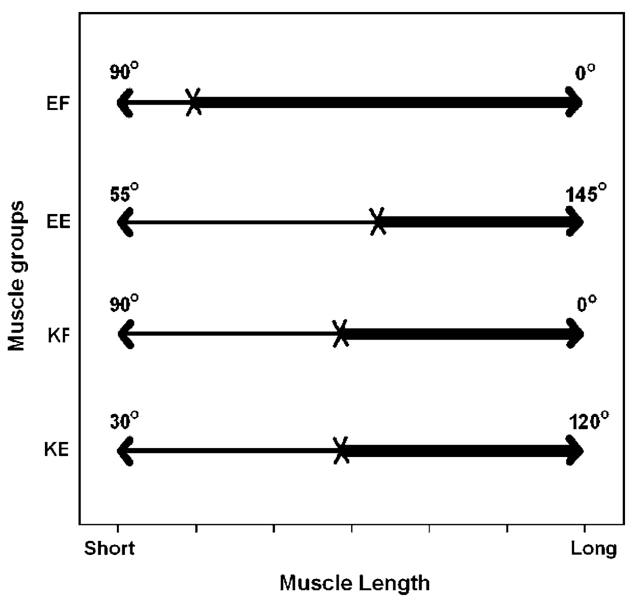

Fig. 8 Possible muscle length changes during eccentric contractions for the given range of motion in the study for the elbow flexors (EF) and extensors (EE), and knee flexors (KF) and extensors (KE) in relation to the estimated optimum angle (shown in *X*). The *thick line* represents the ranges that the muscles were possibly in the descending limb

In terms of muscle architecture, the four muscles in the KE (vastus lateralis, vastus medialis, rectus femoris, and vastus intermedius) have relatively larger penneation angle, shorter muscle fibres, and smaller fibre length/muscle length ratio compared with those of the four muscles (semimembranosus, semitendinosus, biceps femoris long and short heads) in the KF (Becker et al. 2009; Erskine et al. 2009; Makihara et al. 2006; Wickiewicz et al. 1983). The smaller penneation angle and longer muscle length of the KF may make it more susceptible to eccentric exercise-induced muscle damage than KE (Lieber 2002; Orchard and Seward 2002; Slavotinek et al. 2002). It is also possible that larger muscles are less susceptible to eccentric exercise-induced muscle damage than small muscles, as for the case for muscle fatigue such that larger muscles take much greater stress to fatigue than smaller muscles (Hoeger et al. 1987,1990). Although the present study did not assess muscle volume using magnetic resonance or CT scan, generally the volume of the KE is greater than that of the KF (Wickiewicz et al. 1983). However, it does not appear that the susceptibility to muscle damage can be explained by the volume of muscle. For example, no clear symptoms of muscle damage were found for the wrist extensors even following 300 maximal eccentric contractions (Slater et al. 2010). It is also important to note that even for the same muscle, the susceptibility is changed by previous eccentric contractions as explained above (i.e. the repeated bout effect).

A difference in fibre type composition in muscle could also affect the susceptibility to eccentric exercise-induced muscle damage, since it has been shown that type II fibres are more susceptible to eccentric exercise-induced muscle damage than type I fibres (Fridén et al. 1983). Johnson et al. (1973) reported that EE (long head: type I: 33%, type II: 67%) consists of more type II fibres than EF (biceps brachii: type I: 46%, type II: 54%). However, the present study did not find a significant difference in muscle damage between EF and EE. According to the data reported by Johnson et al. (1973), KE appears to have greater type II fibre percentage (type I: 40%, type II: 60%) compared with KF (type I: 60%, type II: 40%). However, the magnitude of muscle damage was greater for KF than EE. The fibre type composition of the subjects involved in the present study is not known; however, it seems unlikely that the subjects involved in the present study were largely different from general population. Thus, it does not appear that fibre type composition could explain the difference in the susceptibility among the muscles.

A large variability among the subjects for their responses to eccentric exercise is seen in the four exercises (Fig. 7). It has been shown that genetic differences exist between "high responders" and "low responders". For example, Clarkson et al. (2005) reported that the subjects with homozygous myosin light chain kinase (MLCK) 49T and heterozygotes for the MLCK C37885A rare allele had significantly elevated CK and Mb following eccentric exercise of the EF. Hubal et al. (2010) have recently reported that variations in single nucleotide polymorphisms (SNPs) in chemokine ligand 2 (CCL2) and its receptor chemokine receptor 2 (CCR2) are associated with the level of muscle soreness, CK responses and strength recovery following eccentric exercise of the EF. However, the susceptibility is muscle specific as shown in the present and previous studies (Jamurtas et al. 2005; Saka et al. 2009; Franklin et al. 1993), and even in the same individuals. As shown in Fig. 7, the subjects who showed large changes in the muscle damage markers for the EF exercise did not necessarily show larger changes in the markers following other exercises. Thus, it does not appear that genetic factors can fully explain the susceptibility to eccentric exercise-induced muscle damage.

It is important to understand that the magnitude of muscle damage induced by eccentric exercise is dependent on muscles. Although many studies used EF as a model, it should be noted that the findings based on the EF model cannot be necessarily applied for other muscles. As clearly shown in the present study, the characteristics of muscle damage are different between arm and leg muscles, as well as between the two leg muscles. Thus, it is ideal to use a specific exercise model of a specific muscle to understand the nature of muscle damage of the muscle on focus, and investigate the effect of an intervention on muscle damage using an appropriate eccentric exercise model.

It is concluded that the muscle damage was similar between EF and EE, but the magnitude of the muscle damage in KF was less than EF and EE, and KE was the least susceptible to eccentric exercise-induced muscle damage amongst the four muscles. It appears that the exposure to eccentric contractions in daily activity is one of the main factors determining the susceptibility. Other factors, such as differences in muscle architecture and muscle length changes during eccentric contractions appear to be contributing factors. It is also important to note that setting the eccentric exercise differently by changing muscle lengths and the number of contractions could result in different magnitude of muscle damage even for the same muscle.

Acknowledgments This research was supported by the National Science Council, Taiwan (NSC 98-2410-H-415-042) and Edith Cowan University, Australia. The authors would like to thanks Professor Tsai-Wei Huang, Department of Counseling at National Chiayi University, for his assistance with the statistical design and analysis.

Conflict of interest The authors declare that they have no conflict of interest.

References

Becker I, Woodley S, Baxter GD (2009) Gross morphology of the vastus lateralis muscle: an anatomical review. Clin Anat 22:436–450

Black CD, McCully KK (2008) Muscle injury after repeated bouts of voluntary and electrically stimulated exercise. Med Sci Sports Exerc 40:1605–1615

Bowers EJ, Morgan DL, Proske U (2004) Damage to the human quadriceps muscle from eccentric exercise and the training effect. J Sports Sci 22:1005–1014

Brockett CL, Morgan DL, Proske U (2001) Human hamstring muscles adapt to eccentric exercise by changing optimum length. Med Sci Sports Exerc 33:783–790

Byrne C, Twist C, Eston R (2004) Neuromuscular function after exercise-induced muscle damage: theoretical and applied implications. Sports Med 34:49–69

Chapman DW, Newton M, McGuigan M, Nosaka K (2008) Effect of lengthening contraction velocity on muscle damage of the elbow flexors. Med Sci Sports Exerc 40:926–933

Chen TC, Nosaka K (2006) Responses of elbow flexors to two strenuous eccentric exercise bouts separated by three days. J Strength Cond Res 20:108–116

Chen TC, Nosaka K, Sacco P (2007) Intensity of eccentric exercise, shift of optimum angle and the magnitude of repeated bout effect. J Appl Physiol 102:992–999

Chen TC, Chen HL, Lin MJ, Wu CJ, Nosaka K (2009) Muscle damage responses of the elbow flexors to four maximal eccentric exercise bouts performed every four weeks. Eur J Appl Physiol 106:267–275

Chelboun GS, France AR, Crill MT, Braddock HK, Howell JN (2001) In vivo measurement of fascicle length and pennation angle of the human biceps femoris muscle. Cells Tissues Organs 169:401–409

Clarkson PM, Hubal MJ (2002) Exercise-induced muscle damage in humans. Am J Phys Med Rehabil 81:S52–S69

Clarkson PM, Nosaka K, Braun B (1992) Muscle function after exercise-induced muscle damage and rapid adaptation. Med Sci Sports Exerc 24:512–520

Clarkson PM, Hoffman EP, Zambraski E, Gordish-Dressman H, Kearns A, Hubal M, Harmon B, Devaney JM (2005) ACTN3 and MLCK genotype associations with exertional muscle damage. J Appl Physiol 99:564–569

Cramer JT, Beck TW, Housh TJ, Massey LL, Marek SM, Danglemeier S, Purkayastha S, Culbertson JY, Fitz KA, Egan AD (2007) Acute effects of static stretching on characteristics of the isokinetic angle-torque relationship, surface electromyography, and mechanomyography. J Sports Sci 25:687–698

Crameri RM, Aagaard P, Qvortrup K, Langberg H, Olesen J, Kjær M (2007) Myofibre damage in human skeletal muscle: effects of electrical stimulation versus voluntary contraction. J Physiol (Lond) 583:365–380

Dudley GA, Czerkawski J, Meinrod A, Gillis G, Baldwin A, Scarpone M (1997) Efficacy of naproxen sodium for exercise-induced dysfunction muscle injury and soreness. Clin J Sport Med 7:3–10

Erskine RM, Jones DA, Maganaris CN, Degens H (2009) In vivo specific tension of the human quadriceps femoris muscle. Eur J Appl Physiol 106:827–838

Franklin ME, Chamness MS, Chenier TC, Mosteller GC, Barrow LA (1993) A comparison of isokinetic eccentric exercise on delayed-onset muscle soreness and creatine kinase in the quadriceps versus the hamstrings. Isokinet Exerc Sci 3:68–73

Fridén J, Sjøstrøm M, Ekblom B (1983) Myofibrillar damage following intense eccentric exercise in man. Int J Sports Med 4(3):170–176

Golden CL, Dudley GA (1992) Strength after bouts of eccentric or concentric actions. Med Sci Sports Exerc 24:926–933
Hawes MR, Martin AD (2001) Human body composition. In: Eston R, Reilly T (eds) Kinanthropometry and exercise physiology laboratory manual: tests, procedures and data. Routledge, London, pp 42–43
Hirose L, Nosaka K, Newton M, Lavender A, Kano M, Peake J, Suzuki K (2004) Changes in inflammatory mediators following eccentric exercise of the elbow flexors. Exerc Immunol Rev 10:75–90
Hoeger WWK, Barette SL, Hale DP, Hopkins DR (1987) Relationship between repetitions and selected percentages of one repetition maximum. J Appl Sport Sci Res 1:11–13
Hoeger WWK, Hopkins DR, Barette SL, Hale DP (1990) Relationship between repetitions and selected percentages of one repetition maximum: a comparison between untrained and trained males and females. J Appl Sport Sci Res 4:47–54
Hubal MJ, Devaney JM, Hoffman EP, Zambraski EJ, Gordish-Dressman H, Kearns AK, Larkin JS, Adham K, Patel RR, Clarkson PM (2010) CCL2 and CCR2 polymorphisms are associated with markers of exercise-induced skeletal muscle damage. J Appl Physiol 108:1651–1658
Johnson MA, Polgar J, Weightman D, Appleton D (1973) Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. J Neurol Sci 18:111–129
Jamurtas AZ, Theocharis V, Tofas T, Tsiokanos A, Yfanti C, Paschalis V, Koutedakis Y, Nosaka K (2005) Comparison between leg and arm eccentric exercises of the same relative intensity on indices of muscle damage. Eur J Appl Physiol 95:179–185
Lieber RL (2002) Skeletal muscle structure, function, and plasticity: the physiological basis of rehabilitation, 2nd edn. Lippincott Williams & Wilkins, Baltimore
Makihara Y, Nishino A, Fukubayashi T, Kanamori A (2006) Decrease of knee flexion torque in patients with ACL reconstruction: combined analysis of the architecture and function of the knee flexor muscles. Knee Surg Sports Traumatol Arthrosc 14:310–317
McHugh MP (2003) Recent advances in the understanding of the repeated bout effect: the protective effect against muscle damage from a single bout of eccentric exercise. Scand J Med Sci Sports 13:88–97
McHugh MP, Connolly DAJ, Eston RG, Gleim GW (1999) Exercise-induced muscle damage and potential mechanisms for the repeated bout effect. Sports Med 27:157–170
Newton MJ, Morgan GT, Sacco P, Chapman DW, Nosaka K (2008) Comparison of responses to strenuous eccentric exercise of the elbow flexors between resistance-trained and untrained men. J Strength Cond Res 22:597–607
Nosaka K, Clarkson PM (1996) Changes in indicators of inflammation after eccentric exercise of the elbow flexors. Med Sci Sports Exerc 28:953–961
Nosaka K, Newton M (2002) Difference in the magnitude of muscle damage between maximal and submaximal eccentric loading. J Strength Cond Res 16:202–208
Nosaka K, Sakamoto K, Newton M, Sacco P (2001) The repeated bout effect of reduced-load eccentric exercise on elbow flexor muscle damage. Eur J Appl Physiol 85(1–2):34–40
Orchard J, Seward H (2002) Epidemiology of injuries in the Australian football league, seasons 1997–2000. Br J Sports Med 36:39–44
Paschalis V, Koutedakis Y, Baltzopoulos V, Mougios V, Jamurtas JZ, Giakas G (2005) Short vs. long length of rectus femoris during eccentric exercise in relation to muscle damage in healthy males. Clin Biomech 20:617–622
Perotto AO (1994) Anatomical guide for the electromyographer: the limbs and trunk, 3rd edn. Charles C Thomas Publisher, Springfield, Illinois
Prior BM, Jayaraman RC, Reid RW, Cooper TG, Foley JM, Dudley GA, Meyer RA (2001) Biarticular and monoarticular muscle activation and injury in human quadriceps muscle. Eur J Appl Physiol 85:185–190
Saka T, Akova B, Yazici Z, Sekir U, Gür H, Ozarda Y (2009) Difference in the magnitude of muscle damage between elbow flexors and knee extensors eccentric exercises. J Sports Sci Med 8:107–115
Slavotinek JP, Verrall GM, Fon GT (2002) Hamstring injury in athletes: using MR imaging measurements to compare extent of muscle injury with amount of time lost from competition. Am J Roentgenol 179:1621–1628
Slater H, Thériault E, Ronningen BO, Clark R, Nosaka K (2010) Exercise-induced mechanical hypoalgesia in musculotendinous tissues of the lateral elbow. Man Ther 15:66–73
Visser JJ, Hoogkamer JE, Bobbert MF, Huijing PA (1990) Length and moment arm of human leg muscles as a function of knee and hip-joint angles. Eur J Appl Physiol Occup Physiol 61:453–460
Wickiewicz TL, Roy RR, Powell PL, Edgerton VR (1983) Muscle architecture of the human lower limb. Clin Orthop Relat Res 179:275–283